Effects of sex and reproductive mode on dietary composition of the reproductively bimodal scincid lizard, *Lerista bougainvillii*

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ABSTRACT

We dissected preserved specimens from both oviparous and viviparous South Australian populations of a fossorial skink *Lerista bougainvillii*, to identify food items and to examine possible effects of sex and reproductive mode on the composition of the diet. There were significant differences in dietary composition (i) between the sexes and (ii) within each sex, between oviparous (Eyre Peninsula, Fleurieu Peninsula) and viviparous (Kangaroo Island) conspecifics. In both populations, females tended to feed primarily on large, surface-active prey (primarily hemipterans) rather than the smaller, secretive prey (especially weevils) that dominated the diets of males. This difference may reflect females' difficulties in penetrating into narrow spaces under cover items: females are the larger sex, and are considerably distended during gestation. Diets also differed between oviparous and viviparous populations, in both sexes, but these differences may reflect local resource availability rather than a direct effect of reproductive mode. Our preliminary analysis suggests that a more detailed study of this question would be worthwhile.

INTRODUCTION

Reproductive biology and foraging ecology may influence each other in complex ways, and squamate reptiles offer ideal model systems in which to investigate this interaction (e.g., Huey and Pianka 1981). For example, viviparity (live-bearing) has arisen from oviparity (egg-laying) at least 100 times within reptile phylogeny (Shine 1985). The evolution of viviparity within a reptile species might affect the animal's seasonal schedules of activity, and the greater distension of the female's body by the offspring (Qualls and Shine, in prep.) may restrict the range of microhabitats in which gravid lizards can forage. These kinds of shifts in the times and places that foraging occurs, could well influence the composition of the diet. The reverse phenomenon may also occur, whereby adaptations of foraging biology modify the reproductive biology of reptiles (Vitt and Congdon 1978). For example, ambush predation may facilitate the evolution of viviparity, because the longer gestation period of viviparous lizards and the greater bodily distension of gravid live-bearers may be less of a "cost" to such species than to a more elongate active forager that relied upon mobility for prey capture and predator escape (Fitch 1970). Either causal pathway could result in trophic differences between oviparous and viviparous female lizards, and between females and conspecific males.

The evolution of viviparity has been a major focus of research in reptilian biology for more than half a century (e.g., Weekes 1933; Tinkle and Gibbons 1977; Shine 1985). Most evolutionary origins of viviparity have been followed by extensive adaptive radiations, so that it is difficult to identify the morphological and ecological characteristics of the organisms in which viviparity arouse. However, a small number of extant squamate species show both oviparous and viviparous reproduction in different parts of their geographic ranges, and hence offer uniquely suitable material with which to investigate the effects of this major evolutionary transition. One such taxon is the elongate, fossorial scincid lizard *Lerista bougainvillii* of southeastern Australia (Fig. 1). Mainland populations in New South Wales, Victoria and South Australia reproduce by egg-laying, but island populations in two areas (Bass Strait/Tasmania and Kangaroo Island) bear fully-formed live young (Greer 1989; Qualls *et al.* 1994). The South Australian populations of *L. bougainvillii* are particularly well-suited to comparisons between egg-laying and live-bearing conspecifics, because the live-bearing animals on Kangaroo Island are separated by <20 km from egg-laying lizards of the same species on the Eyre and Flerieu Peninsulas (Qualls *et al.* 1994). Morphological, electrophoretic and DNA-sequence studies have confirmed that the oviparous and

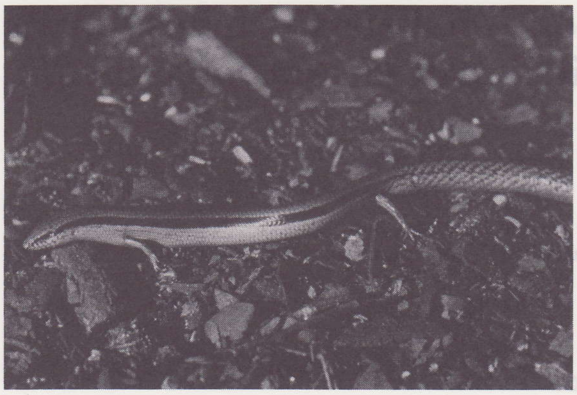

Figure 1. An adult *Lerista bougainvillii* (photo by C. Qualls). Note the small head and limbs, and elongate body of this fossorial lizard.

viviparous populations within this species are closely related (Fairbairn 1993; Qualls *et al.* 1994).

As is the case with most Australian lizard species (Greer 1989; but see Lunney *et al.* 1989), there have been no quantitative analyses of dietary habits in *Lerista bougainvillii.* We examined and identified gut contents of specimens from the area in South Australia where both reproductive modes occur, to (i) describe the general diet of this species, and (ii) examine the effects of gender and reproductive mode on the kinds of prey items consumed.

MATERIALS AND METHODS

The lizards we used for these analyses were preserved specimens in the collections of the Australian Museum and South Australian Museum. The lizards examined ranged from 32 to 62 mm snout-vent length. All of the viviparous animals ($n = 9$ males, 4 females) came from Kangaroo Island, and the egg-layers ($n = 15$ males, 17 females) came from the nearby Eyre Peninsula ($n = 28$) and Fleurieu Peninsula ($n = 4$). The gut contents were removed through a midventral incision, and then identified using available taxonomic keys. The resultant data are shown in Table 1, which presents the data separately according to sex and reproductive mode of the lizards. We estimated the importance of each prey taxon in two ways: as a proportion of all prey items found in that group of lizards (sorted by gender and reproductive mode — e.g., males of the oviparous populations), and as a proportion of all prey-occurrence records in lizards in that group (so that multiple prey items within a single lizards counted as only one record). The latter method reduces biases that can arise if a few individuals contain very large numbers of a particular prey type.

RESULTS

First, we report body sizes of the lizards from which prey items were identified. A two-factor analysis of variance, with sex and reproductive modes as the factors, and snout-vent length (=SVL, in mm) as the dependent variable, showed that there was a highly significant difference in mean body size between the sexes ($F_{1,50} = 22.3$, $P < 0.0001$), but no overall difference in body size between oviparous and viviparous populations ($F_{1,50} = 0.40$, $P = 0.53$), and no difference in the degree of sexual size dimorphism between the two geographic areas sampled ($F_{1,50} = 0.02$, $P = 0.88$). Combining data from both areas, males (mean = 45.9 mm SVL, SD = 6.79) were much smaller than conspecific females (mean = 54.9 mm, SD = 4.57).

All of the prey items identified were invertebrates. The most important prey taxa numerically, in terms of total numbers of prey as well as the numbers of lizards eating that prey, were beetles (Coleoptera). These constituted >40 per cent of the prey items identified from each of our four groups of lizards, and >20 per cent of all prey-type occurrences within each group of lizards (Table 1). Within the Coleoptera, the Curculionidae (weevils) was the most important taxon (>20% of prey items in each group, >20% of prey-occurrence records). A single species of weevil of the genus *Sclerorinus* was the major contributor to these numbers, constituting >16 per cent (and up to 47%) of prey items within each group of lizards, and >19 per cent (up to 26%) of prey-occurrence records. The next most important group were bugs (Hemiptera), especially in female rather than male *L. bougainvillii* (Table 1). Most other groups of invertebrates were taken only rarely, although lizards from Kangaroo Island contained significant numbers of pseudoscorpions (Table 1).

Our two methods of scoring importance generally yielded similar results, although some differences were apparent. For example, coleopterans constituted 73 per cent of all prey items from mainland male lizards, but only 52 per cent of prey-occurrence records from this group (Table 1). This difference reflects a tendency for multiple meals: lizards with coleopterans in their stomachs had often eaten several specimens. Contingency-table tests were used to compare the relative frequences of different prey types between sexes and between reproductive models (we did not compare prey-occurrence categories because sample sizes were too low for adequate statistical power). Results were as follows:

(i) *Gender.* Males and females differed in dietary composition in the oviparous (mainland) population ($\chi^2 = 38.1$, 10 df, $P < 0.001$). A similar difference between the sexes was evident in the viviparous population, but the lower sample size meant that this difference did not attain statistical significance ($\chi^2 = 19.8$, 13 df, $P = 0.10$).

(ii) *Reproductive mode.* Because of the significant sex difference documented above, we analysed data separately for the two sexes. Significant differences between oviparous and viviparous populations were evident in both males ($\chi^2 = 36.6$, 14 df, $P < 0.001$) and females ($\chi^2 = 51.5$, 9 df, $P < 0.001$).

DISCUSSION

Our data set is preliminary in nature, because it is based on very small sample sizes collected over a long time period. Nonetheless, the data in Table 1 are sufficient to reveal some interesting trends.

(i) The relatively high proportion of prey items unidentifiable to the familial level reflects the well-macerated condition of the stomach contents in this species. Our subjective impression from bites incurred when handling live animals, is that the jaws of *Lerista bougainvillii* are far more powerful than are those of similar-sized skinks such as *Lampropholis* or *Morethia*. In particular, the prevalence of weevils (Curculionidae) is a tribute to the powerful jaws of these tiny lizards. Weevils are exceptionally hard-bodied prey and we suspect that most small skinks of other species would by unable to crush their exoskeletons. Although some weevils had been swallowed entire or had been broken into discrete body segments (along existing suture lines), rather than crushed, close examination of ingested weevils showed that their sclerites were usually cracked.

(ii) The breadth of the diet suggests that *L. bougainvillii* are relatively unselective with respect to the prey items they will eat, and that these lizards forage in a variety of microhabitats. In this respect *L. bougainvillii* resemble other small Australian skinks such as *Lampropholis guichenoti* and *L. delicata* (Lunney *et al.* 1989). The coleopterans ingested are probably taken mostly under cover items, where they

Table 1. Prey items identified from stomach contents of semi-fossorial scincid lizards, *Lerista bougainvillii* from South Australia. The table provides data on the number of prey items (absolute values, and as a percentage of all prey items identified from that group of lizards) and on the number of lizards containing they prey type (absolute numbers, and as a percentage of all prey-type occurrences of lizards within that group). Common names from Naumann (1993).

		By number of prey items:				By number of lizards:			
		Oviparous		Viviparous		Oviparous		Viviparous	
Prey taxon	Common name	male	female	male	female	male	female	male	female
Coleoptera	beetles	36 (73%)	48 (46%)	14 (45%)	5 (42%)	12 (52%)	14 (48%)	8 (38%)	4 (44%)
Curculionidae	weevils	29 (59%)	34 (32%)	7 (23%)	3 (25%)	8 (35%)	9 (31%)	5 (24%)	2 (22%)
Cantharidae	soldier beetles	0	7 (7%)	1 (3%)	0	0	1 (3%)	1 (5%)	0
Cryptophagidae		0	0	1 (3%)	0	0	0	1 (5%)	0
Chrysomelidae	leaf beetles	1 (2%)	1 (1%)	0	0	1 (4%)	1 (3%)	0	0
Cucujidae (larvae)		0	0	2 (6%)	0	0	0	1 (5%)	0
Unidentified		6 (12%)	6 (6%)	3 (10%)	2 (17%)	5 (22%)	6 (22%)	2 (10%)	2 (22%)
Hemiptera	bugs	6 (12%)	54 (51%)	1 (3%)	6 (50%)	2 (9%)	9 (31%)	1 (5%)	4 (44%)
Cydnidae	burrowing bugs	0	0	1 (3%)	1 (8%)	0	0	1 (5%)	1 (11%)
Pentatomidae	shield bugs	6	41 (39%)	0	1 (8%)	2 (9%)	7 (24%)	0	1 (11%)
Lygaeidae	seed bugs	0	12 (11%)	0	0	0	2 (7%)	0	0
Unidentified		0	1 (1%)	0	4 (33%)	0	1 (3%)	0	2 (22%)
Other Insecta									
Formicidae	ants	1 (2%)	3 (3%)	1 (3%)	0	1 (4%)	2 (7%)	1 (5%)	0
Lepidoptera (pupae)	caterpillars	0	0	2 (6%)	0	0	0	1 (5%)	0
Thysanoptera	thrips	0	0	2 (6%)	0	0	0	2 (10%)	0
Unidentified		2 (4%)	0	1 (3%)	0	2 (9%)	0	1 (5%)	0
Arachnida									
Pseudoscorpiones	pseudoscorpions	0	0	7 (23%)	1 (8%)	0	0	4 (19%)	1 (22%)
Araneida	spiders	1 (2%)	0	0	0	1 (4%)	0	0	0
Mollusca									
Gastropoda	snails	3 (6%)	0	3 (10%)	0	1 (4%)	0	1 (5%)	0
Totals		49	105	31	12	23	29	21	9

hide, but the hemipterans are more likely to be taken when they are active, in more open habitats. These powerful fast-moving skinks probably have little difficulty in overpowering even formidable prey such as spiders.

(iii) The consistent tendency for female *L. bougainvillii* to take more hemipterans than do males (in both oviparous and viviparous populations: Table 1) may reflect either size selection (hemipterans tend to be larger than coleopterans) or, more likely, differences between the two sexes in foraging microhabitats. Females are larger than males in this species (see above) and hence may take larger prey: such a correlation has been documented in many other types of reptiles (e.g., Shine 1991). Alternatively, the sexes may diverge in foraging microhabitats, if the larger females are less able to fit under close-fitting cover objects to take coleopterans, and concentrate instead on taking surface-active prey (such as hemipterans) in more open areas. The considerable bodily distension of gravid females — especially in the viviparous population — might exacerbate the females' difficulty in penetrating narrow crevices under cover items. Interestingly, a recent study of the small terrestrial African Skink *Mabuya acutilabris* found an identical sex difference, whereby females took higher proportions of hemipterans, and lower proportions of coleopterans, than did conspecific males (Castanzo and Bauer 1993).

We refrain from drawing any firm conclusions about the biological significance of apparent (i.e., statistically significant) effects of gender and reproductive mode on the dietary composition in *L. bougainvillii* for two reasons. Firstly, our sample sizes are low, especially for the viviparous animals, and further data are needed to support or rebut our tentative conclusions on dietary variation within this species. Secondly, any differences that *do* exist between oviparous and viviparous populations may well result from geographic differences in prey availability between the island and mainland populations, rather than from a direct effect of reproductive mode. The composition of the diet may be very sensitive to such proximate factors, rather than invariant through space and time (e.g., Lunney *et al.* 1989). Nonetheless, our preliminary analysis has revealed consistent intraspecific differences, associated with reproductive mode and gender, suggesting that a more extensive study on this topic would be worthwhile. Ideally, such a study should incorporate comparisons among other populations of *L. bougainvillii*, especially between the viviparous Bass Strait/Tasmanian animals and their nearest oviparous (Victorian) conspecifics. It should also incorporate measurements of prey availability in the different habitats, to allow an assessment of the degree to which geographic differences in dietary composition reflect some attribute of the study animal (e.g., reproductive mode) versus a direct influence of geographic differences in prey availability.

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REFERENCES

Castanzo, R. A. and Bauer, A. M., 1993. Diet and activity of *Mabuya acutilabris* (Reptilia: Scincidae) in Namibia. *Herpetol. J.* **3:** 130–35.

Fairbairn, J., 1993. *The maternal phylogeny of a reproductively bimodal skink.* B.Sc. Hons Thesis, School of Biological Sciences, Sydney University.

Fitch, H. S., 1970. Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 52: 1–247.

Greer, A. E., 1989. *The Biology and Evolution of Australian Lizards.* Surrey Beatty & Sons: Chipping Norton.

Huey, R. B. and Pianka, E. R., 1981. Ecological consequences of foraging mode. *Ecology* **62:** 991–99.

Lunney, D., Ashby, E., Grigg, J. and O'Connell, M., 1989. Diets of scincid lizards *Lampropholis guichenoti* (Dumeril and Bibron) and *L. delicata* (De Vis) is Mumbulla State Forest on the south coast of New South Wales. *Aust. Wildl. Res.* **16:** 307–12.

Naumann, I. D. (ed), 1993. *CSIRO Handbook of Australian Insect Names. Common and Scientific Names for Insects and Allied Organisms of Economic and Environmental Importance.* Sixth Edition, Govt. Publisher: Sydney.

Qualls, R., Shine, R., Donnellan, S. and Hutchinson, M., 1994. The evolution of viviparity within the Australian scincid lizard *Lerista bougainvillii*. *J. Zool. (London)* in press.

Shine, R., 1985. The evolution of viviparity in reptiles: an ecological analysis. Pp. 605–94 in *Biology of the Reptilia, Volume 5* ed by C. Gans and F. Billett. John Wiley and Sons: New York.

Shine, R., 1991. Why do larger snakes eat larger prey? *Funct. Ecol.* **5:** 493–502.

Tinkle, D. W. and Gibbons, J. W., 1977. The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool., Univ. Michigan* **154:** 1–55.

Vitt, L. J. and Congdon, J. D., 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112:** 595–608.

Weekes, H. C., 1933. On the distribution, habitat and reproductive habits of certain European and Australian snakes and lizards, with particular regard to their adoption of viviparity. *Proc. Linn. Soc. NSW* **58:** 270–74.